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VOLATILE ALLELOCHEMICALS RELEASED BY CRUCIFER GREEN MANURES[1]

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Abstract—Several members of the crucifer family (Brassicaceae), including white mustard (*Brassica hirta* Moench), brown mustard [*B. juncea* (L.) Coss], black mustard [*B. nigra* (L.) Koch], leafy turnip (*B. campestris* L.), rapeseed (*B. napus* L.), and garden cress (*Lepidium sativum* L.) were examined for their potential as allelopathic green manure crops. Hemp sesbania [*Sesbania exaltata* (Raf.) Rydb. Ex A. W. Hill] germination and fresh weight was inhibited by chopped leaf tissues of all green manures tested, including wheat (*Triticum aestivum* L.), when added to a sandy loam soil. Wheat seed germination was inhibited only by *B. nigra*, *B. hirta*, and *L. sativum*, although none of the treatments reduced fresh weight of germinated seedlings. The major volatiles released by chopped plants were determined by solid-phase microextraction sampling and identified by gas chromatography–mass spectrometry (GC-MS). Volatiles included allyl isothiocyanate (allyl-ITC), 3-butenyl isothiocyanate, benzyl isothiocyanate (benzyl-ITC), *cis*-3-hexen-1-ol, and *trans*-2-hexenal. These compounds, together with methyl-ITC (methyl-ITC), β-phenylethyl-ITC, benzaldehyde, β-ocimene, and α-farnesene were tested for inhibition of seed germination of several crop and weed species when applied as volatiles. Of these, allyl-ITC and methyl-ITC were the most inhibitory, completely inhibiting the germination of all species at a headspace gas concentration of 1 ppm in airtight glass containers. Selecting mustard green manures that release high levels of allyl-ITC would appear to be optimal for allelopathic activity, and plants that produce high levels of benzyl-ITC also appear promising.

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[1] Propietary names are necessary to report factually on available data; however, the USDA neither guarantees nor warrants the standard of the product, and the use of the name by USDA implies no approval of the product to the exclusion of others that may also be suitable.

Key Words—*Brassica campestris, Brassica hirta, Brassica juncea, Brassica napus, Brassica nigra, Lepidium sativum*, allyl isothiocyanate, benzyl isothiocyanate, methyl isothiocyanate, volatiles, phytotoxicity, allelopathy.

INTRODUCTION

The Brassicaceae, or crucifer family, is a large plant family that includes important food crops, ornamentals, and weeds (Lawrence, 1951). Crucifers have generated much interest for their potential as green manures or soil amendments for the suppression of weeds (Brown and Morra, 1995; Grossman, 1993; Boydston and Hang, 1995), soil pathogens (Papavizas, 1996; Lewis and Papavizas, 1971; Papavizas and Lewis, 1971; Ramirez-Villapudua and Munnecke, 1988; Muelchen et al., 1990; Mayton et al., 1996), nematodes (Mojtahedi et al., 1991, 1993), and insects (Brown et al., 1991). The pesticidal activity of crucifers has been thought to be due primarily to glucosinolates and their degradation products. Glucosinolates are a class of glucose- and sulfur-containing compounds whose biologically active degradation products are produced when the plant cells are ruptured and the glucosinolates present in vacuoles are hydrolyzed by the enzyme myrosinase (β-thioglucosidase glucohydrolase; EC 3.2.3.1) (VanEtten and Tookey, 1983). These products include substituted isothiocyanates (ITC), nitriles, thiocyanates, and oxazolidinethiones, which vary depending on the side-chain substitution, pH, and iron concentration (Cole, 1976; Daxenbichler and VanEtten, 1977; Fenwick et al., 1983; Uda et al., 1986; Borek et al., 1994, 1995). Several volatile ITCs, including allyl (2-propenyl)-ITC (allyl-ITC), 2-phenylethyl-ITC, and benzyl-ITC have been shown to be toxic to a wide range of organisms at relatively low molar concentrations (Wolf et al., 1984; Bialy et al., 1990; Lazzeri et al., 1993; Williams et al., 1993). Because ITCs are relatively insoluble in water, their activity would be in the vapor phase as volatiles. In addition to glucosinolate degradation products, other volatiles would be expected to be released when crucifer green manures are incorporated into the soil, notably products of the lipoxygenase pathway, which include (*E*)-2-hexenal, (*Z*)-3-hexen-1-ol, and (*Z*)-3-hexen-1-yl acetate (Gardner, 1995). These compounds were among the major volatiles produced by disrupted tissues of several crucifers (Wallbank and Wheatley, 1976; Tollsten and Borgström, 1988), and they have been shown to be toxic as volatiles to plants (Gardner et al., 1990; Bradow, 1991), fungi (Hamilton-Kemp et al., 1992; Doehlert et al., 1993; Gamliel and Stapleton, 1993; Vaughn and Gardner, 1993; Zeringue et al., 1996), and bacteria (Croft et al., 1993; Deng et al., 1993).

We are examining several members of the Brassicaceae as green manure crops to suppress weeds, including white mustard (*Brassica hirta* Moench), brown mustard [*B. juncea* (L.) Coss], black mustard [*B. nigra* (L.) Koch], leafy turnip (*B. campestris* L.), rapeseed (*B. napus* L.), and garden cress (*Lepidium sativum* L.). Our objectives were to evaluate their potential to suppress weed emergence and growth when green tissues were incorporated into soil, to determine the major volatiles released by chopped tissues, and to determine the relative toxicities of these volatiles against several bioassay species.

METHODS AND MATERIALS

Plant Material. Crucifers examined were *B. juncea* Greenwave, *B. juncea* Florida Broadleaf, *B. campestris* L. Seven Top, *B. napus* L. Jupiter, *B. hirta* Moench Martigeña, and *L. sativum* L. Curly Cress. *B. nigra* seed used was a wild population collected near Peoria, Illinois. Wheat (*Triticum aestivum* L. Cardinal), which has shown little or no weed suppression in field tests, was used as a green manure control. Plants were grown in a growth chamber at a 16 hr 26°C day/8 hr 21°C night for 30 days before leaf and stem tissues were harvested.

Germination and Growth of Wheat and Hemp Sesbania in Soil with Incorporated Plant Tissues. Green manure plants grown in the growth chamber were harvested, chopped into 0.5-cm^2 pieces, and uniformly mixed into soil (Onarga sandy loam; Typic Argiudoll) at a rate of 0.05 g of plant material/ g soil. The plant–soil mixture was added to 200-ml cups, and 10 seeds of either wheat or hemp sesbania (species that we have found to be good indicators of suppressive activity in bioassays) were added and covered with approximately 2 cm of the mixture. Nonamended soil was used as the control. Each cup received 10 ml of a solution containing 1 g/liter thiabendazole (TBZ; 10 mg/cup) to inhibit soil fungi, which were found to inhibit soil germination of the test species. Additional water was added to bring the cups to field capacity, and the plants were placed in the growth chamber at the same conditions as before. Cups were watered daily to field capacity, with the soil becoming dry near the surface between waterings. Germination and fresh weight (aboveground tissue only) were measured 10 days after planting. Each green manure treatment was replicated five times per species, and the experiment was repeated. Treatment means were separated using Fisher's protected LSD test at the 5% level (StatView, Abacus Concepts, Berkeley, California).

Volatile Analysis. Five grams of plant material were shredded with a food chopper and placed rapidly in 2.4-liter glass desiccators equipped with 3-mm holes through which rubber septa were fitted. After 15 min, a solid-phase microextraction (SPME) device (Supelco, Inc., Bellefonte, Pennsylvania) with a 100-μm polydimethylsiloxane coating was inserted through the septa and allowed to absorb volatiles for 1 min. Absorbed compounds were desorbed at

200°C onto the inlet injector for 0.5 min on a Hewlett-Packard (HP) 5890 Series II gas chromatograph (Hewlett-Packard Co., Palo Alto, California) equipped with a flame ionization detector, and peaks were analyzed by an HP 3396 integrator. The column used was a fused silica DB-1 capillary (0.25-μm film thickness, 15 m $\times$ 0.25 mm ID; J & W Scientific, Folsom, California). Mass spectra were produced by introducing samples through a HP 6890 gas chromatograph connected to a HP 5973 mass selective detector. The column used was a HP-5MS capillary (30.0 m $\times$ 0.25 mm ID, 0.25-μm film thickness). Compounds were identified by comparison of mass spectra with pure standards, with a library data base, and/or with previously published spectra for glucosinolate degradation products (Spencer and Daxenbichler, 1980).

Effect of Volatiles on Crop and Weed Seed Germination. The five volatiles found in the highest concentrations by SPME were allyl-ITC, 3-butenyl-ITC, benzyl-ITC, *cis*-hexen-1-ol, and *trans*-2-hexenal. Other volatiles examined were β-phenylethyl-ITC, benzaldehyde, β-ocimene, and α-farnesene, which have been reported as major volatiles released from either intact and disrupted tissues of several *Brassica* species (Tollsten and Bergström, 1988). These compounds were tested for inhibition of seed germination of corn (*Zea mays* L.), soybeans [*Glycine max* (L.). Merr.], wheat, rapeseed, cucumber (*Cucumis sativus* L.), alfalfa (*Medicago sativa* L.), and dandelion (*Taraxacum officinale* Weber in Wiggers) when applied as volatiles, with the commercial soil fumigant methyl-ITC included as a reference standard. Ten seeds of each species were placed in 9-cm petri dishes on Whatman No. 1 filter paper saturated with sterile distilled water. These dishes were placed in 2.4-liter desiccator flasks containing a 9-cm filter paper disk to which test compounds were added on a volume compound–headspace volume basis at rates of 1.0, 5.0, and 10.0 ppm. Each flask was fitted with a septum allowing the headspace volatiles to be sampled by SPME. Flasks were placed in darkness in a growth chamber at 25°C for four days, after which germination was scored. Each treatment was replicaed three times and the experiment was repeated.

RESULTS AND DISCUSSION

Germination and Growth of Wheat and Hemp Sesbania with Incorporated Green Manures. Hemp sesbania and wheat were markedly different in their response to soil-incorporated green manure tissues (Table 1). Hemp sesbania emergence and growth were reduced by every green manure treatment, including incorporated wheat. In several of the green manure treatments (*B. campestris* Seven Top, *B. hirta* Martigeña, *B. juncea* Greenwave, *B. nigra* and *L. sativum* Curly Cress) hemp sesbania seedling emergence, and hence growth, was zero. Conversely, wheat emergence was suppressed to a much lower extent, and only

TABLE 1. EMERGENCE AND GROWTH OF WHEAT AND HEMP SESBANIA IN SOIL WITH MACERATED GREEN MANURE LEAF AND STEM TISSUES[a]

Green manure	Hemp sesbania (% of control)		Wheat (% of control)	
	Emerged seedlings	Fresh weight	Emerged seedlings	Fresh weight
None	100.0a	100.0a	100.0a	100.0cd
B. campestris				
Seven Top	0.0d	0.0d	84.8c	105.8c
B. hirta Martigeña	0.0d	0.0d	78.2d	91.6e
B. juncea				
Florida Broadleaf	4.4c	4.7c	100.0a	126.7a
B. juncea Greenwave	0.0d	0.0d	93.6b	97.2d
B. napus Jupiter	4.2c	3.0c	93.6b	112.7b
B. nigra	0.0d	0.0d	84.8c	105.8c
Lepidium sativum				
Curly Cress	0.0d	0.0d	69.4e	95.0de
Triticum aestivum				
Cardinal	72.2b	61.3b	100.0a	108.6bc

[a]Means within a column followed by the same letter are not different at $P = 0.05$ according to Fisher's protected LSD test.

the *B. hirta* Martigeña treatment significantly inhibited growth relative to the control, with growth promotion occurring with incorporated *B. juncea* Florida Broadleaf and *B. napus* Jupiter tissues. Boydston and Hang (1995) found similar results when they incorporated leaf tissues of rapeseed or potato into a sandy loam soil. Hairy nightshade (*Solanum sarrachoides* Sendtner) seedling emergence and growth were inhibited by both rapeseed and potato tissues, but longspine sandbur [*Cenchrus longispinus* (Hack.) Fern.] emergence and growth were only reduced by the rapeseed treatment. The authors observed that hairy nightshade was suppressed by the addition of all of the biomasses tested, while longspine sandbur was not. The physical impacts of a biomass acting as a mulch may have contributed to inhibition in field plots, as Putnam et al. (1983) found that popular excelsior (which had been found to have no adverse effect on plants in the greenhouse), although not affecting weed seed germination, reduced weed biomass in field plots, possibly by shading and/or cooling of the soil.

Volatiles Released by Macerated Tissues. Although there were substantial differences between the volatiles collected by SPME from the different green manures, there were also several similarities (Table 2). With the exception of *B. campestris* and wheat, one volatile accounted for >50% of the total volatiles collected. In all cases, the dominant compounds were either products of glu-

TABLE 2. RELATIVE CONCENTRATIONS OF MAJOR VOLATILES RELEASED BY MACERATED GREEN MANURE LEAF AND STEM TISSUES

Species	Volatile	% of total volatiles collected by SPME[a]
B. campestris Seven Top	*cis*-3-hexen-1-yl acetate	27.2
	3-butenyl isothiocyanate	21.5
	cis-3-hexen-1-ol	19.8
B. hirta Martigeña	benzyl isothiocyanate	84.0
	cis-3-hexen-1-ol	8.7
B. juncea Florida Broadleaf	allyl isothiocyanate	67.7
	trans-2-hexenal	8.6
B. juncea Greenwave	allyl isothiocyanate	67.3
	trans-2-hexenal	17.7
B. napus Jupiter	*cis*-3-hexen-1-yl acetate	78.5
	cis-3-hexen-1-ol	13.9
B. nigra	allyl isothiocyanate	54.4
	cis-3-hexen-1-yl acetate	12.7
Lepidium sativum Curly Cress	benzyl isothiocyanate	56.9
	benzaldehyde	7.0
Triticum aestivum Cardinal	*trans*-2-hexenal	26.6
	cis-3-hexen-1-ol	20.2
	cis-3-hexen-1-yl acetate	11.2

[a]Values represent the mean percentages of three replicates. Only compounds comprising >5% of total volatiles are presented.

cosinolate degradation (allyl-, 3-butenyl-, and benzyl-ITC) or were lipoxygenase pathway metabolites [(E)-2-hexenal, (Z)-3-hexen-1-ol, and (Z)-3-hexen-1-yl acetate]. Allyl-ITC was the major volatile from both of the brown mustard cultivars as well as the black mustard tissues, while benzyl-ITC was the major compound released from white mustard and garden cress. Tollsten and Bergström (1988) found a similar volatile profile, although in their study the volatiles from macerated leaf tissues were captured on a porous polymer (Porapak Q) instead of SPME. Although β-hydroxy-substituted glucosinolates have been reported in several of the species examined (Daxenbichler et al., 1991) and are especially high in rapeseed (Brown et al., 1991), their degradation products (oxazolidinethiones) were not detected with SPME sampling, probably due to low volatilities for these compounds.

Inhibition of Seed Germination by Volatiles. Methyl-ITC and allyl-ITC were the most inhibitory compounds tested, with I_{50} values of less than 1 ppm for all of the species tested (Table 3). 3-Butenyl-ITC was as toxic as methyl-

TABLE 3. I_{50} VALUES FOR INHIBITION OF GERMINATION OF SEEDS EXPOSED TO GREEN MANURE VOLATILES

Volatile	I_{50} (ppm)[a]						
	Soybean	Corn	Wheat	Rapeseed	Dandelion	Alfalfa	Cucumber
Methyl-ITC	< 1	< 1	< 1	< 1	< 1	< 1	< 1
Allyl-ITC	< 1	< 1	< 1	< 1	< 1	< 1	< 1
3-Butenyl-ITC	< 1	< 1	< 1	> 5	< 1	< 1	< 1
Benzyl-ITC	> 10	> 10	> 10	> 10	< 1	< 1	> 10
2-Phenylethyl-ITC	> 10	> 10	> 10	> 10	> 10	> 10	> 10
Benzaldehyde	> 5	> 10	> 5	> 5	< 1	> 1	> 10
trans-2-Hexenal	> 1	> 5	> 5	> 1	< 1	> 1	> 10
cis-3-Hexen-1-ol	> 5	> 5	> 5	> 5	> 1	< 1	> 10
cis-3-Hexen-1-yl acetate	> 5	> 5	> 1	> 1	< 1	> 1	> 5
β-Ocimene	> 10	> 10	> 10	> 10	> 10	> 10	> 10
α-Farnesene	> 10	> 10	> 10	> 10	> 10	> 10	> 10

[a] I_{50} values represent the mean of three replicates.

ITC and allyl-ITC to every species except rapeseed, for which the I_{50} value was > 5 ppm. This may be due to metabolism of 3-butenyl-ITC by the rapeseed, as it has been shown to contain the parent 3-butenyl glucosinolate (Daxenbichler et al., 1991; Brown et al., 1991). The much lower levels of activity shown by benzyl-ITC and 2-phenylethyl-ITC were somewhat surprising. 2-Phenylethyl-ITC was the most phytotoxic isothiocyanate tested against wheat seed germination (Bialy et al., 1990), while benzyl-ITC constitutes the major volatile released by both *B. hirta* Martigeña and *L. sativum* Curly Cress, the most inhibitory green manure treatments to wheat seed germination used in this study. The decreased activities of these two compounds may be due to their lower volatilities (therefore decreasing the headspace concentrations) in comparison to methyl-ITC and allyl-ITC. The lipoxygenase pathway volatiles, *trans*-2-hexenal, *cis*-3-hexen-1-ol, and *cis*-3-hexen-1-yl acetate, were intermediate in activity, exhibiting the lowest activity against cucumber, a species that has been reported to possess high lipoxygenase activity (Matsui et al., 1992; Avdiushko et al., 1994; Gardner, 1995). Both α-farnesene and β-ocimene, volatiles reportedly released from intact leaves of *Brassica* spp. (Tollsten and Bergström, 1988), were the least phytotoxic compounds tested, with I_{50} values of > 10 ppm for all species tested.

Volatiles released by crushed leaves of *B. juncea* and *B. nigra* inhibited seed germination of lettuce (*Lactuca sativa* L.), barnyardgrass [*Echinochloa* *crus-galli* (L.) Beauv.], and wheat (Oleszek, 1987). In our study, the major volatile compound released by both species was allyl-ITC. Although benzyl-ITC was less toxic than allyl-ITC to seeds in the glass desiccators, two of the green manures with the most activity (*B. hirta* and *L. sativum*) released benzyl-ITC as their primary volatile. The lower activity of benzyl-ITC in the desiccator study can be explained by its much lower volatility [allyl-ITC has a vapor pressure of 5 mm Hg at 25°C while benzyl-ITC has a vapor pressure of < 1 at this temperature (Jordan, 1954)]. Perhaps in the soil–plant mixture higher levels of benzyl-ITC were reached as compared to inside the desiccators. Teasdale and Taylorson (1986) reported that methyl-ITC was more toxic to large crabgrass [*Digitaria sanguinalis* (L.) Scop.] when applied to soil containing crabgrass seeds rather than when the seeds were directly exposed to a methyl-ITC solution. Another possibility is a synergy of several different compounds, which, as Einhellig (1987) has pointed out, appears to be the norm in allelopathic interactions.

While it appears from our data that commercially acceptable suppression of weeds using crucifer green manures is unlikely, their use may allow reduced or delayed herbicide use in conventional systems and may be especially helpful for organic production systems where tillage is the major weed control method. We have observed that crucifer green manures can delay weed seed germination and emergence in field trials. Selecting crucifer green manures with higher allyl and benzyl glucosinolate levels than those tested in this study may provide adequate weed suppression if combined with tillage and (reduced) use of herbicides.

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